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Epigenetic variation in the human cranium

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INTRODUCTION

This paper is concerned with the description and racial incidence of minor morphological variations in the human skull. Although such variants can be found in every system in the body, this study is confined to those which occur in the cranium, because of the large amount of available material.

The variants we have studied can seldom be stigmatized as abnormal—indeed some are so common that it may be difficult to know what is the 'normal' condition. Despite this, they tend to be neglected by anatomists and most of them are recognized only by mentions in anatomical text-books, being described in terms such as 'rare' or 'occasionally found'. Nevertheless, a few of them have been utilized as anthropological markers, e.g. persistence of the medio-frontal suture; mandibular, auditory and maxillary tori; imperfect transverse foramina of the cervical vertebrae (reviewed by Brothwell, 1963, 1965).

Some variants are the consequence of disease or other extrinsic influences. For example, Møller-Christensen & Sandison (1963) have shown fairly conclusively that osteopetrosis of the orbit is the result of pathological changes; Roche (1964) has distinguished two types of aural exostosis, one at least being the sequel of some factor like masticatory stress or otitis media; and Dorsey (1897) has claimed that artificial deformation of the cranium by 'head-binding' tends to lead to intercalary bones in affected sutures. However, there are three reasons for believing that most of these variants result from normal developmental processes and are genetically determined:

(1) Family studies on some of these traits have shown them to be inherited, usually 'by a dominant gene with incomplete penetrance' (e.g. Montagu, 1937; Torgensen, 1952; Selby, Garn & Kanareff, 1955; Grahnèn, 1956; Suzuki & Sakai, 1960; Johnson, Gorlin & Anderson, 1965).

(2) The frequency of any particular variant is constant in a given race, and is similar in related races. Indeed, geographical 'isoincidence lines' can be constructed for a variant in the same way that blood-group frequency maps can be drawn (Brothwell, 1958). Chambellan (1883) seems to have been the first to suggest the possibility of using such traits as anthropological characters. He made a study of sutural bones. Russell (1900) gathered together data on a number of skull variants in American groups and gave the first indication of their use in the comparison of populations. About the same time Le Double (1903, 1906, 1912) was also collecting a vast amount of data on variations in both skull and vertebral column. Wood-Jones

(1930–31, 1933–34) used data on skull variants in a more systematic comparison of a number of Far Eastern groups, and, more recently, Laughlin & Jorgensen (1956), Brothwell (1958) and Laughlin (1963) have attempted to make such comparisons quantitative.

(3) Grüneberg and his co-workers have described variants in the skeleton of the mouse (reviewed by Grüneberg, 1963) which are morphologically analogous to those which occur in man. In inbred strains of mice any one variant has a constant incidence which can be changed by mutational events (Deol, Grüneberg, Searle & Truslove, 1957), i.e. these variants are inherited. However, crosses between strains do not give rise to Mendelian segregation ratios for the variants in the progeny. This is because the actual inherited entity is the size (or rate of formation) of an embryonic rudiment and not the presence or absence of a variant in the mature skeleton. Now the size of any particular rudiment is variable at the same stage in different individuals. If the structure regresses through being too small for further development, the result is a variant. For example, 18 % of CBA mice lack one or both their lower third molars. Grüneberg (1951) showed that the inherited character was tooth *size* and not tooth *loss*: if the tooth germ is too small, the tooth fails to develop. Although there can be no certainty that these mouse variants are developmentally the same as similar ones in the human skeleton, it would seem unreasonable to suppose that their genetical basis is completely different.

Grüneberg (1952) devised the name 'quasi-continuous' for the variants he worked upon in the mouse. This name describes the two processes involved in their determination: the underlying continuous variable which is influenced by the action of a number of genes; and the discontinuity imposed by the existence of alternative possible end-results of development which is the *epigenetic* consequence of interaction or competition between different developmental processes. The second, epigenetic, component can be affected to some degree by non-genetic influences such as parity or maternal physiology (Searle, 1954*a*, *b*; Deol & Truslove, 1957), but this does not mean that these quasi-continuous variants are not inherited entities. Indeed, a variant may segregate in the different members of a human family so as to mimic Mendelian inheritance, but these cases can be interpreted most easily as being due to a chance association of allelomorphs in that particular family. The developmental genetics of the variants in the mouse show that it is incorrect to think of them as being determined by single gene loci (Berry, 1967). It is the *incidence* of a variant in a population that is a genetical characteristic and not its segregation in a family.

Population studies on epigenetic variants in mice and men

Epigenetic variants are an expression of the genes affecting development. This means that differences in the incidences of variants in different populations almost certainly reflect genetical differences between those populations. Furthermore, there are in the mouse very few correlations of the joint occurrence of pairs of variants. This means that variant differences in a pair of populations can be summed and used as a measure of genetical distinctiveness or divergence between that pair of populations. This approach has been used in the study of genetical changes in laboratory mice with some success (Deol *et al.* 1957; Grewal, 1962; Searle, 1964). One of us (R. J. B.) has shown that populations of mice caught in the wild can be individually

characterized by this method, and that relationships between populations (even including deductions about the past movements of groups of animals) can be assessed (Berry, 1963, 1964).

A number of anthropologists have used epigenetic variants in the past, but they have tended to have an inadequate understanding of the genetical determinants. We undertook this study to determine the availability and extent of epigenetic variation in human material, and to test whether the multivariate statistical methods developed for use in the mouse can reasonably be applied to the analysis of human data. The work involved the description of as many variants as possible which can be scored with reasonable objectivity as present or absent, and the classification of these variants in series of skulls of sufficient number to arrive at fair estimates of the incidences. Anderson (1967) has recently reviewed epigenetic variants in post-cranial material.

MATERIAL AND METHODS

Most of the classification was carried out in the Subdepartment of Anthropology of the British Museum (Natural History), and also in the Duckworth Laboratory, University of Cambridge. Our aim was to classify series of skulls from all the major 'races', although from limited geographical areas within each (i.e. areas such that all the samples might be expected to derive from an inter-breeding group). We also made use of the considerable collections available of ancient Egyptian skulls to test the stability of individual variant frequencies over a long period of time, and to assess the genetical impact of immigration into Egypt from prehistoric to Christian times.

We have examined 585 adult crania. All juveniles were excluded in this investigation. The origins of the skulls were:

(1) *South America:* 53 Amerindians from a number of burial grounds in Peru.

(2) *North America:* 50 Amerindians collected in the neighbourhood of Vancouver, British Columbia.

(3) *Burma:* 51 skulls collected in the neighbourhood of Moulmein in the southern part of Burma. Measurements of these skulls have been published by Tildesley (1920–21).

(4) *North India:* 53 skulls, part of Lt.-Col. Sir R. H. Charles's collection from the Punjab

(5) *Nigeria:* 56 Ashanti, part of the Williamson collection.

(6) *Palestine (modern):* 18 skulls of fairly recent date collected from Tell Farar in 1927–28.

(7) *Palestine (Lachish):* 54 skulls from a very large collection from Lachish (30 miles south-west of Jerusalem) which was partially destroyed by Sennacherib in 701 B.C. It is thought that this material dates from that time (Risdon, 1939).

(8) *Egypt:* It was possible to separate six populations of skulls of different antiquities extending over a period of over 4000 years. All the material was from middle Egypt. Most of the skulls we classified were subjected to extensive biometric analysis in the 1920's and 1930's by G. M. Morant and his co-workers at University College London (key reference: Morant, 1925; most recent publication: Batrawi & Morant, 1947). A comparison of the earlier work with our results will be the subject of a separate communication with Dr P. J. Ucko.

(i) *Badarian* (earlier than 4000 B.C.)—28 skulls.

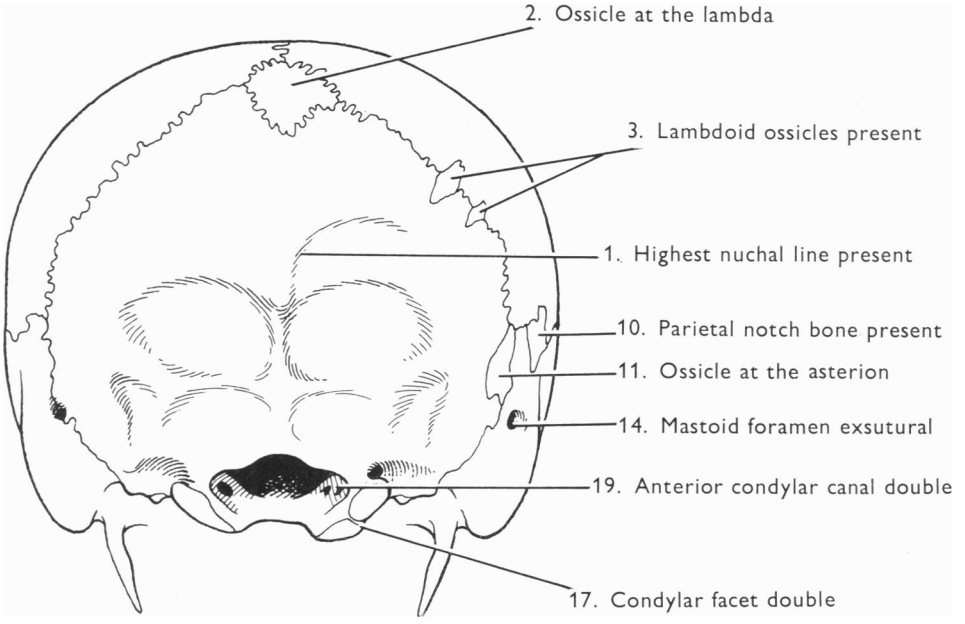
(ii) *Late pre-dynastic* (before 3100 B.C.)—36 skulls from El Amrah and Abydos.

(iii) *Early dynasties* (*I–IV*: 3200 to *c.* 2500 B.C.)—29 skulls from Regagnah, Abydos and El Amrah.

(iv) *Dynasties XII–XVIII* (1800–1500 B.C.)—55 skulls from Gurob, Hou, El Amrah, Shekh Ali and Abydos.

(v) *Dynasties XXVI–XXX* (650–350 B.C.)—50 skulls from Gizeh (part of the 'E' series of 1726 skulls sent to Karl Pearson by Flinders Petrie).

(vi) *Early Christian* (A.D. 200)—52 skulls from the cemetery at Hawara, dating from Roman times.



Figs. 1–6. Drawings of the skull to illustrate the variants described in the text. Where possible both expressions (i.e. 'presence' and 'absence') of a variant are shown, but only one alternative has been labelled.

Fig. 1. Posterior aspect of the skull.

Every skull was classified for thirty variants. Most of these are 'classical' variants described by Wood-Jones (1930–31) and Brothwell (1963); nos. 1, 14, 17, 22 and 25 (see below) were gleaned from *Gray's Anatomy* and have not, as far as we know, been used by previous workers. It was impossible to use some of the published variants (such as the presence or absence of styloid processes) because of the condition of the skulls we used. All the skulls were classified by one of us (A. C. B.).

1. *Highest nuchal line present* (Fig. 1).

The inferior and superior nuchal lines form well-marked ridges running horizontally across the occipital bone. A third line (the highest) is sometimes present. It arises with the superior at the external occipital protuberance, and arches anteriorly and laterally, providing attachment for the epicranial eponeurosis. It is more easily felt than seen.

2. *Ossicle at the lambda* (Figs. 1, 2)

A bone may occur at the junction of the sagittal and lambdoid sutures (the position of the posterior fontanelle). We have described this as an ossicle, and made no attempt to distinguish between a sutural bone in this position, and a 'true' interparietal or Inca bone formed from the membraneous part of the occiput. According to Wood-Jones this latter is very rare.

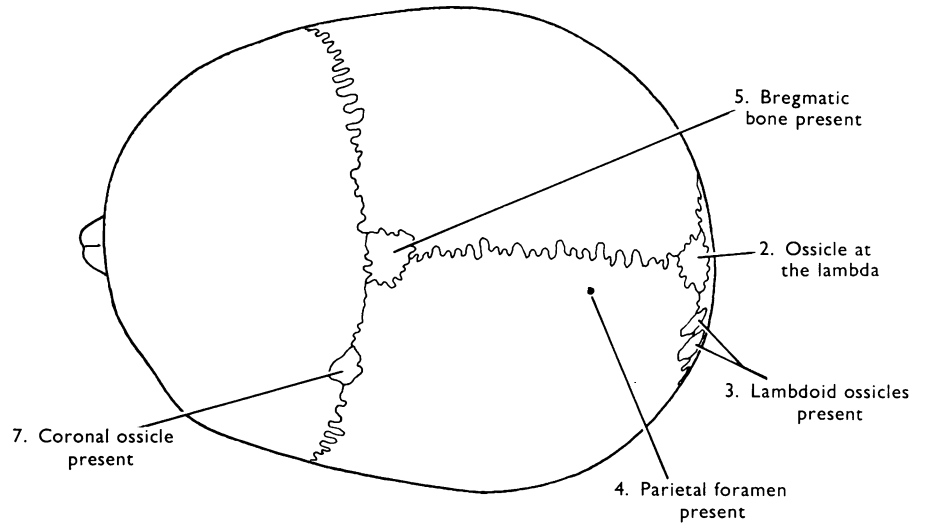


Fig. 2. The skull viewed from above.

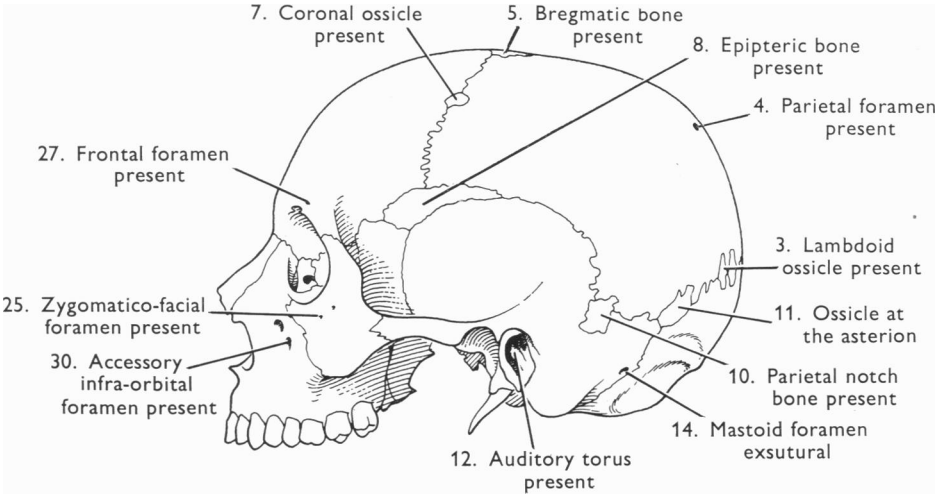


Fig. 3. Left lateral aspect of the skull.

3. *Lambdoid ossicle present* (Figs. 1–3)

One or more ossicles may occur in the lambdoid suture. Up to about twelve distinct bones may be present on either side.

4. *Parietal foramen present* (Figs. 2, 3)

This pierces the parietal bone near the sagittal suture a few centimetres in front of the lambda. It transmits a small emissary vein, and sometimes a small branch of the occipital artery.

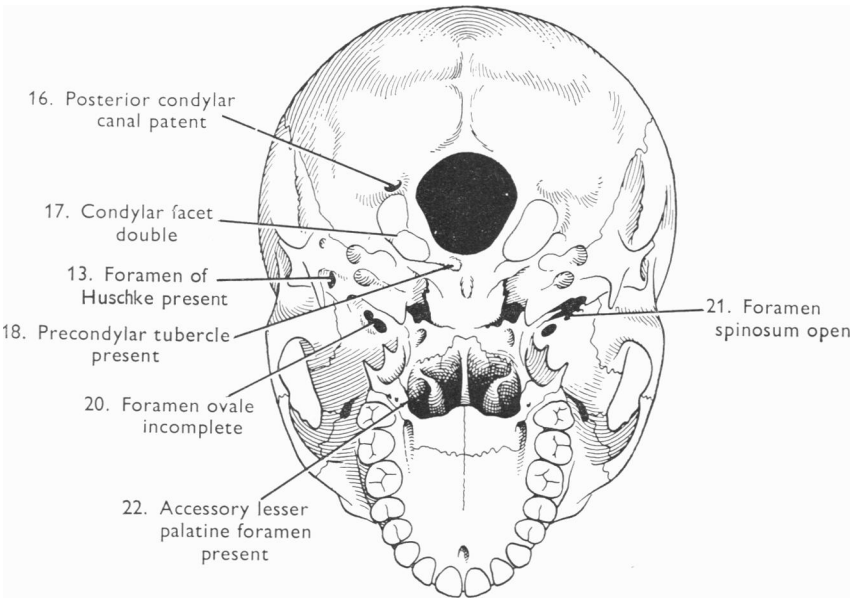


Fig. 4. The skull viewed from below.

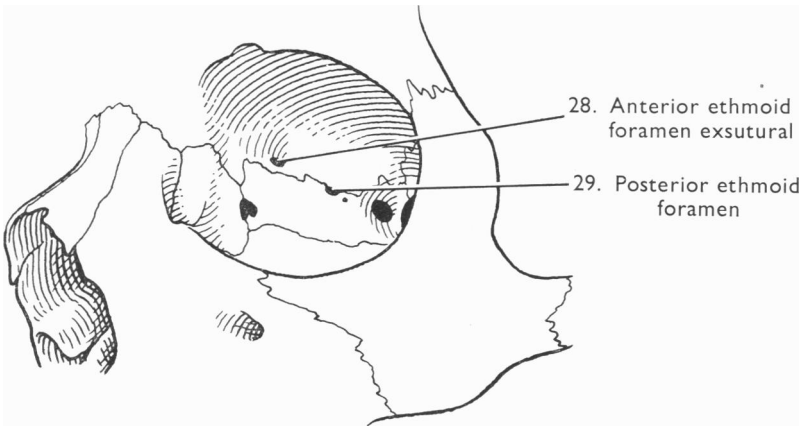


Fig. 5. Fronto-lateral aspect of the left orbit to show sutures and foramina.

5. *Bregmatic bone present* (Figs. 2, 3)

A sutural bone (the bregmatic or interfrontal) may occur at the junction of the sagittal suture with the coronal one (the position of the anterior fontanelle).

6. *Metopism* (Fig. 6)

The medio-frontal suture disappears within the first two years of life. In a few individuals it persists throughout life: this condition is known as metopism.

7. *Coronal ossicle present* (Figs. 2, 3, 6)

Ossicles are sometimes found in the coronal suture.

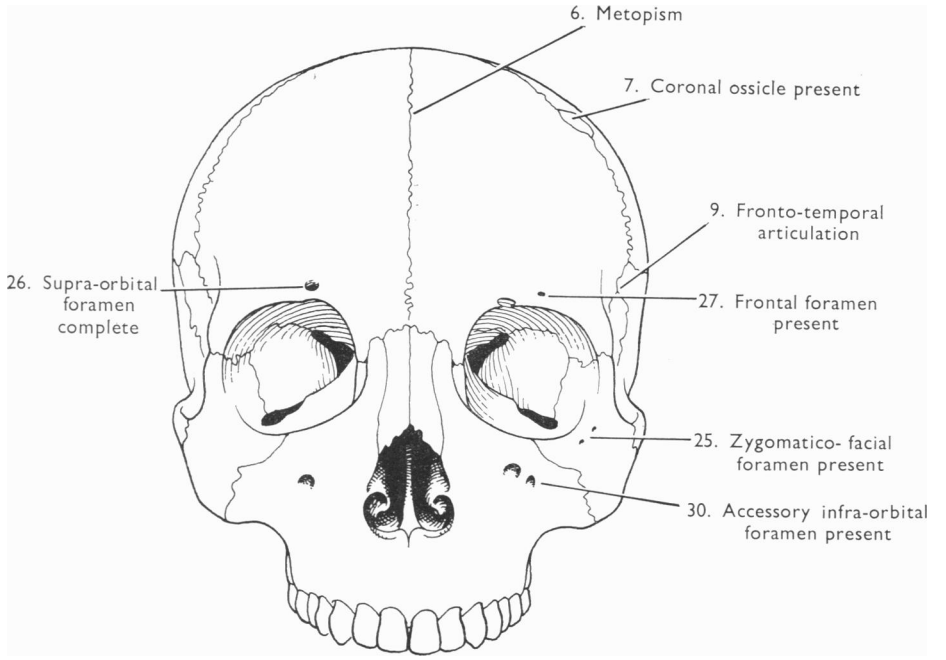


Fig. 6. Facial aspect of the skull.

8. *Epipteric bone present* (Fig. 3)

A sutural bone (the epipteric bone or pterion ossicle) may be inserted between the anterior inferior angle of the parietal bone and the greater wing of the sphenoid. When large it may also articulate with the squamous part of the temporal bone.

9. *Fronto-temporal articulation* (shown, not very clearly, on Fig. 6, left side)

Normally the frontal bone is separated from the squamous part of the temporal bone by the greater wing of the sphenoid and the anterior inferior angle of the parietal bone. Occasionally the frontal and temporal bones are in direct contact, forming a fronto-temporal articulation.

10. *Parietal notch bone present* (Figs. 1, 3)

The parietal notch is that part of the parietal bone that protrudes between the squamous and the mastoid portions of the temporal bone. It may form a separate ossicle which is known as the parietal notch bone.

11. *Ossicle at asterion* (Figs. 1, 3)

The junction of the posterior inferior angle of the parietal bone with the occipital bone and mastoid portion of the temporal bone is known as the asterion. A sutural bone may occur at this junction.

12. *Auditory torus present* (Fig. 3)

Rarely a bony ridge or torus is found on the floor of the external auditory meatus.

13. *Foramen of Huschke present* (Fig. 4)

This is a foramen occurring in the floor of the external auditory meatus. It is always present in young children but only occasionally does it persist after the fifth year. It is most easily scored from the inferior aspect of the tympanic part of the temporal bone.

14. *Mastoid foramen exsutural* (Figs. 1, 3)

15. *Mastoid foramen absent*

When present, the mastoid foramen usually lies in the suture between the mastoid part of the temporal bone and the occipital bone. Less frequently it lies exsuturally, piercing the mastoid part of the temporal bone, or, more rarely, the occipital bone.

16. *Posterior condylar canal patent* (Fig. 4)

The posterior condylar canal usually pierces the condylar fossa which lies immediately posterior to the occipital condyle. Sometimes it ends blindly in the bone, and has only been scored as patent when a seeker can be passed through it. Scoring this character is unsatisfactory in skulls in poor condition because the bone of the condylar fossa is often fragile, so that a patent canal and a broken fossa are indistinguishable.

17. *Condylar facet double* (Figs. 1, 4)

Occasionally the articular surface of the occipital condyle is divided into two distinct facets.

18. *Precondylar tubercle present* (Fig. 4)

Occasionally a bony tubercle lies immediately anterior and medial to the occipital condyle. A centrally placed tubercle has been regarded as two fused tubercles.

19. *Anterior condylar canal double* (Fig. 1)

This canal (foramen hypoglossi) pierces the anterior part of the occipital condyle and transmits the hypoglossal nerve. Embryologically the nerve originates from

several segments and this may result in the canal being divided into two for part or all of its length. This is most easily scored by looking inside the foramen magnum.

20. *Foramen ovale incomplete* (Fig. 4)

Rarely the postero-lateral wall of the foramen ovale is incomplete so that the foramen is continuous with the foramen spinosum.

21. *Foramen spinosum open* (Fig. 4)

The posterior wall of the foramen spinosum is sometimes deficient. (This is another character difficult to score in skulls in poor condition.)

22. *Accessory lesser palatine foramen present* (Fig. 4)

The lesser palatine foramina lie on both sides of the posterior border of the hard palate immediately posterior to the greater palatine foramen, and transmit the lesser palatine nerves. When more than one (there may be three or four) foramen is present, it has been scored as accessory.

23. *Palatine torus present* (not illustrated)

Rarely, a bony ridge runs longitudinally down the mid-line of the hard palate. This is the palatine torus. Although it occurs in *c.* 10 % of British skulls (Brothwell, 1963), it was seen only once among the 600 skulls classified in this study (see Discussion).

24. *Maxillary torus present* (not illustrated)

The maxillary torus is a bony ridge running along the lingual aspects of the roots of the molar teeth. It was not seen in this study.

25. *Zygomatico-facial foramen absent* (Figs 3, 6)

This is a small foramen which pierces the zygomatic bone opposite the junction of the infraorbital and lateral margins of the orbit. It transmits a nerve and small artery, and may be single, multiple or absent.

26. *Supraorbital foramen complete* (Figs. 3, 6)

The supraorbital foramen transmits the supraorbital vessels and nerve. It is frequently incomplete (or open). In this case it is often described as a 'supraorbital notch'.

27. *Frontal notch or foramen present* (Figs. 3, 6)

A well-defined secondary foramen in the vicinity of (usually lateral to) the supraorbital foramen has been scored as a frontal foramen. Frequently a cluster of tiny foramina are present, but these have been ignored. However, scoring was inevitably somewhat arbitrary in a few border-line cases.

28. *Anterior ethmoid foramen exsutural* (Fig. 5)

The anterior ethmoid foramen pierces the medial wall of the orbit. It normally lies on the suture between the medial edge of the orbital plates of the frontal and ethmoid bones, but it occasionally emerges above the suture.

29. *Posterior ethmoid foramen absent* (Fig. 5)

The posterior ethmoid foramen lies just behind the anterior ethmoid foramen on the same suture line. Its absence can only be scored satisfactorily in well-preserved skulls.

30. *Accessory infraorbital foramen present* (Figs. 3, 6)

A second foramen may lie immediately adjacent to the infraorbital foramen.

RESULTS

The incidence of the thirty variants in the skulls classified are set out in Tables 1 and 2. In both tables data from males and females have been combined as there are no sex differences in the incidences of the variants (see below). Where specimens were damaged, the incidence is based on the number of skulls in which classification was possible. A lateral variant may occur on either or both sides in any skull, so the incidence is based on the number of occurrences of such characters. Differences between the different Egyptian populations were not large (although see below) and they have been pooled into a single population in Table 1.

There are two ways of interpreting the data in the tables. The first is to take each variant separately and trace its incidence in different populations. This has been the normal procedure with past workers and has resulted in much information about the distribution of some variants (e.g. Hess, 1945; Brothwell, 1958). Examination of the tables shows that there is a wide range of frequencies for many characters (e.g. nos. 16 and 22 vary between 13 and 70 %), while others are fairly stable (no. 8 ranges only between 6 and 18 %). Many of the differences in incidence of individual variants between populations are formally significant, but such tests do not give any very useful information for most purposes.

A more digestible method of assimilating the crude data is to calculate a multivariate distance statistic based on all the variants. There are several ways of doing this: Laughlin & Jorgensen (1956) and Brothwell (1958) have used a variation of Penrose's 'size and shape' statistic, but we prefer a method devised by C. A. B. Smith and first used by Grewal (1962). In this method a single 'measure of divergence' is calculated between every pair of populations. The genetical validity of the method is discussed by Berry & Smith (1967).

STATISTICAL ANALYSIS

The measure of divergence between two populations (1, 2) of size n_1 and n_2 is taken as $(\theta_1-\theta_2)^2-(1/n_1+1/n_2)$ for any character where θ is the angular transformation of the percentage incidence (p), measured in radians, such that $\theta = \sin^{-1}(1-2p)$. This

Table 1. *Incidence of skeletal non-metrical variants in samples from eight human populations*

Number of skulls classified ...	Egypt (Summed) 250	Nigeria (Ashanti) 56	Palestine (Lachish) 54	Palestine (Modern) 18	India (Punjab) 53	Burma 51	North America (British Columbia) 50	South America (Peru) 53
	%	%	%	%	%	%	%	%
1. Highest nuchal line present	52/500 10·4	4/112 3·6	18/108 16·7	8/36 22·2	14/106 13·2	13/102 12·8	40/100 40·0	4/106 3·8
2. Ossicle at the lambda	37/250 14·8	7/56 12·5	6/54 11·1	4/18 22·2	11/53 20·7	7/51 13·7	14/50 28·0	9/53 16·9
3. Lambdoid ossicle present	161/499 32·3	29/112 25·9	32/107 29·8	12/36 33·3	34/106 32·1	30/102 29·5	54/100 54·0	48/106 45·2
4. Parietal foramen present	221/500 44·2	57/96 59·2	38/108 35·2	8/36 22·2	53/106 50·0	51/102 50·0	62/100 62·0	56/106 53·0
5. Bregmatic bone present	2/250 0·8	0/56 0	0/53 0	0/18 0	0/53 0	0/51 0	0/50 0	0/53 0
6. Metopism	18/250 7·2	0/56 0	4/54 7·4	1/18 5·5	3/53 5·7	0/51 0	1/50 2·0	1/53 1·9
7. Coronal ossicle present	13/498 2·6	0/111 0	4/108 3·7	0/34 0	2/106 1·9	1/102 1·0	32/100 32·0	2/106 1·9
8. Epipteric bones present	70/487 14·4	7/112 6·2	10/105 9·5	2/31 6·4	18/106 16·9	15/102 14·7	12/100 12·0	8/106 7·5
9. Fronto-temporal articulation	10/489 2·0	11/112 9·8	1/106 0·9	3/31 9·7	2/106 1·9	3/102 3·0	1/100 1·0	2/106 1·9
10. Parietal notch bone present	37/498 7·4	7/112 6·2	3/108 2·8	4/36 11·1	8/106 7·5	8/102 7·8	10/100 10·0	12/106 11·3
11. Ossicle at asterion	64/497 12·9	16/112 14·3	7/108 6·5	3/36 8·3	9/106 8·5	10/102 9·8	19/100 19·0	15/106 14·2
12. Auditory tori present	0/493 0	0/112 0	0/101 0	0/33 0	0/106 0	0/102 0	9/100 9·0	0/106 0
13. Foramen of Huschke present	69/494 14·0	34/112 30·4	18/95 18·9	2/33 6·0	24/106 22·6	25/102 24·5	32/100 32·0	49/106 46·3
14. Mastoid foramen exsutural	190/496 38·3	41/111 36·9	25/108 23·2	12/36 33·3	49/106 46·3	47/102 46·0	42/100 42·0	42/106 39·6
15. Mastoid foramen absent	62/496 12·5	17/111 15·3	42/108 38·8	7/36 19·4	19/106 17·9	8/102 7·8	22/100 22·0	8/106 7·5
16. Posterior condylar canal patent	204/480 42·5	38/112 33·9	40/104 38·5	4/30 13·3	44/106 41·5	45/100 45·0	69/100 69·0	75/106 70·5
17. Condylar facet double	1/485 0·2	1/112 0·9	0/104 0	1/36 2·8	0/106 0	1/97 1·0	1/98 1·0	0/106 0
18. Precondylar tubercle present	34/496 6·9	2/112 1·8	6/106 5·6	0/32 0	6/106 5·6	10/102 9·8	0/98 0	0/106 0
19. Anterior condylar canal double	82/494 16·6	13/112 11·6	7/100 7·0	3/36 8·3	19/106 17·9	10/102 9·8	24/100 24·0	29/106 27·4
20. Foramen ovale incomplete	7/487 1·4	4/112 3·6	2/106 1·9	0/35 0	4/106 3·8	8/98 8·2	6/100 6·0	1/106 0·9
21. Foramen spinosum open	76/475 16·0	8/112 7·1	13/88 14·8	2/25 8·0	14/106 13·2	10/98 10·2	11/100 11·0	20/106 18·9
22. Accessory lesser palatine foramen present	228/469 48·6	46/112 41·0	12/91 13·2	7/30 23·3	51/106 48·0	31/97 32·0	71/100 71·0	63/106 59·4
23. Palatine torus present	0/248 0	0/56 0	0/53 0	0/18 0	0/53 0	0/51 0	1/50 2·0	0/53 0
24. Maxillary torus present	0/498 0	0/112 0	0/105 0	0/36 0	0/106 0	0/102 0	0/100 0	0/106 0
25. Zygomatico-facial foramen absent	94/478 19·3	20/107 18·7	30/100 30·0	13/34 38·2	29/104 27·9	18/101 17·8	32/99 32·3	26/104 25·0
26. Supra-orbital foramen complete	56/500 11·2	13/111 11·7	19/108 17·6	7/34 20·6	13/106 12·3	14/102 13·7	53/100 53·0	32/106 30·2
27. Frontal notch or foramen present	161/500 32·2	34/112 30·4	20/108 18·5	7/34 21·0	34/106 32·0	33/102 32·4	40/100 40·0	48/106 45·3
28. Anterior ethmoid foramen exsutural	101/455 22·2	17/110 15·4	2/26 7·7	7/26 26·9	27/106 25·5	20/78 25·6	50/100 50·0	65/105 62·0
29. Posterior ethmoid foramen absent	17/464 3·7	0/112 0	0/16 0	0/23 0	0/106 0	0/85 0	0/100 0	2/106 1·9
30. Accessory infraorbital foramen present	23/489 4·7	7/110 6·4	3/102 2·9	2/31 6·4	7/105 6·7	7/93 7·5	6/100 6·0	14/106 13·2

Table 2. *Incidence of non-metrical variants in Egyptian skulls of different antiquities*

Number of skulls classified	Badarian 28		Predynastic 36		Early dynasties 29		Dynasties XII–XVIII 55		Dynasties XXVI–XXX 50		Christian 52	
		%		%		%		%		%		%
1. Highest nuchal line present	6/56	10·7	14/72	19·4	3/58	5·2	6/110	5·5	13/100	13·0	10/104	9·6
2. Ossicle at the lambda	3/28	10·7	5/36	13·9	9/29	31·0	8/55	14·5	5/50	10·0	7/52	13·5
3. Lambdoid ossicle present	21/56	37·5	23/71	32·4	26/58	44·8	27/110	24·5	37/100	37·0	27/104	26·0
4. Parietal foramen present	15/56	26·8	28/72	38·9	33/58	56·9	62/110	56·4	38/100	38·0	45/104	43·3
5. Bregmatic bone present	0/28	0	0/36	0	0/29	0	0/55	0	0/50	0	2/52	3·8
6. Metopism	1/28	3·6	3/36	8·3	4/29	13·8	2/55	3·6	5/50	10·0	3/52	5·8
7. Coronal ossicle present	1/56	1·8	4/70	5·7	1/58	1·7	0/110	0	5/100	5·0	2/104	1·9
8. Epipteric bones present	12/53	22·6	4/66	6·1	9/55	16·4	18/109	16·5	8/100	8·0	19/104	18·3
9. Fronto-temporal articulation	0/54	0	1/67	1·5	0/55	0	1/109	0·9	6/100	6·0	2/104	1·9
10. Parietal notch bone present	5/56	8·9	7/70	10·0	5/58	8·6	12/110	10·9	5/100	5·0	3/104	2·9
11. Ossicle at asterion	7/56	12·5	10/69	14·5	12/58	20·7	17/110	15·5	14/100	14·0	4/104	3·8
12. Auditory tori present	0/56	0	0/67	0	0/58	0	0/108	0	0/100	0	0/104	0
13. Foramen of Huschke present	6/56	10·7	13/70	18·6	6/56	10·7	13/108	12·0	15/100	15·0	16/104	15·4
14. Mastoid foramen exsutural	16/54	29·6	17/72	23·6	27/56	48·2	41/110	37·3	37/100	37·0	52/104	50·0
15. Mastoid foramen absent	8/54	14·8	14/72	19·4	4/56	7·1	13/110	11·8	13/100	13·0	10/104	9·6
16. Posterior condylar canal patent	15/50	30·0	38/62	61·3	21/55	38·2	44/109	40·4	37/100	37·0	49/104	47·1
17. Condylar facet double	0/54	0	0/59	0	0/58	0	0/110	0	1/100	1·0	0/104	0
18. Precondylar tubercle present	3/56	5·4	2/68	2·9	1/58	1·7	2/110	1·8	13/100	13·0	13/104	12·5
19. Anterior condylar canal double	8/56	14·3	6/66	9·1	9/58	15·5	15/110	13·6	22/100	22·0	22/104	21·2
20. Foramen ovale incomplete	1/55	1·8	1/62	1·6	2/56	3·6	0/110	0	1/100	1·0	2/104	1·9
21. Foramen spinosum open	11/47	23·4	2/58	3·4	9/56	16·1	12/110	10·9	27/100	27·0	15/104	14·4
22. Acc. lesser palatine foramen present	7/43	16·3	14/56	25·0	24/58	41·4	63/108	58·3	49/100	49·0	71/104	68·3
23. Palatine torus present	0/28	0	0/34	0	0/29	0	0/55	0	0/50	0	0/52	0
24. Maxillary torus present	0/56	0	0/70	0	0/58	0	0/110	0	0/100	0	0/104	0
25. Zygomatico-facial foramen present	12/52	23·1	11/65	16·9	12/56	21·4	25/103	24·3	19/100	19·0	15/102	14·7
26. Supra-orbital foramen open	8/56	14·3	7/72	9·7	3/58	5·2	11/110	10·0	12/100	12·0	15/104	14·4
27. Frontal notch or foramen present	4/56	7·1	26/72	36·1	18/58	31·0	43/110	39·1	26/100	26·0	44/104	42·3
28. Anterior ethmoid foramen exsutural	17/47	36·2	15/51	29·4	14/50	28·0	21/107	19·6	17/96	17·7	17/103	16·5
29. Posterior ethmoid foramen absent	0/40	0	7/58	12·1	3/54	5·6	2/108	1·9	5/100	5·0	0/104	0
30. Accessory infraorbital foramen present	1/56	1·8	2/67	3·0	2/57	3·5	4/107	3·7	7/99	7·1	7/103	6·8

has the advantage over the more usual angular transformation ($\theta = \sin^{-1}\sqrt{p}$ in degrees) that the variance of θ in a sample of size n is nearly $1/n$ independently of the value of n, instead of $820{\cdot}7/n$. The mean 'measure of divergence' for all thirty characters in two populations is a quantitative expression of the separation of the populations.

This computation has the additional property that since θ has the variance $1/n$, $\theta_1 - \theta_2$ has variance $1/n_1 + 1/n_2 = V$, and where there is no real difference between the large populations from which the two samples are drawn, the observed $\theta_1 - \theta_2 = D$ will be a nearly normal deviate with mean zero and variance V. Thus $(\theta_1 - \theta_2)^2/V$ will be approximately distributed as χ^2 with one degree of freedom; and it will be significant at, for example, the 0·05 probability level if it is greater than $3V$, and at the 0·01 level if it is greater than $6V$.

The variance of D^2 will be approximately $4D^2 \times$ variance of D

$$= 4D^2\,(1/n_1 + 1/n_2) \text{ for any pair of characters,}$$

$$= 4\,(1/n_1 + 1/n_2)\Sigma D^2 \text{ for any pair of populations.}$$

Thus an estimate of the variance of the mean measure of divergence between two populations classified for 30 variants is given by

$$4\,(1/n_1 + 1/n_2)\,\Sigma[(\theta_1 - \theta_2)^2 - (1/n_1 + 1/n_2)]/30.$$

A major objection to summing individual values is that this procedure treats all values as statistically independent and takes no account of the correlation, or covariance, of different variants in the same skull. The effect of such associations would be to cause very high or very low values of the mean measure of divergence to occur more frequently by chance than they should, and hence invalidate much of their potential use as measures of genetical separation (Fisher, 1936). It was important, therefore, to test for the presence and strength of any correlations between the characters we used. The task of extracting data and calculating correlation coefficients was performed by electronic computer on the classifications of 99 Egyptian skulls from Gizeh and Hawara, this being a sufficiently large sample to reveal any but the smallest associations. Two characters showed no variation in this series, so correlation was effectively tested between 378 pairs of characters. Only ten pairs were significantly correlated at approximately the 1 % probability level (correlation coefficient/its standard error > 2·5) and none of them were very highly significant (Table 3). Since about four correlations would be expected by chance from this number of comparisons, these ten significant values can best be interpreted as showing extremely little inter-correlation particularly since four of the ten involve variation at the lambda or in the lambdoid suture. Furthermore, there was no trend towards association among the 368 non-significant correlation coefficients which were calculated: 184 of these showed positive correlation, 184 negative. This extremely low level of correlation between different epigenetic variants bears out the findings of Truslove (1961) in a similar study on the mouse. In genetical terms it must mean that the variants classified are the pleiotropic manifestations of many independent developmental processes, and that differences in the 'spectrum' of epigenetic variation between individuals reveals variation at a large number of gene loci.

The virtual absence of correlation between variants makes it permissible to sum

individual measures of divergence without having to perform the complex adjustments necessary in computing similar statistics from skeletal measurements, which tend to be much more highly correlated. Accordingly, the mean measures of divergence and their standard deviations between all the pairs of populations listed in Tables 1 and 2 have been calculated and are given in Tables 4 and 5. The modern

Table 3. *Correlation coefficients (r) between pairs of skull variants where r/S.E. (r) > 2·5*

Variant	r
Supra-orbital foramen open – ossicle at the lambda	−0·31
Lambdoid ossicle present – ossicle at the lambda	+0·31
Lambdoid ossicle present – parietal notch bone present	+0·27
Lambdoid ossicle present – metopism	+0·31
Condylar facet double – metopism	+0·34
Coronal ossicle present – fronto-temporal articulation	+0·36
Coronal ossicle present – foramen spinosum open	+0·25
Parietal foramen present – foramen ovale incomplete	+0·27
Posterior ethmoid foramen absent – foramen ovale incomplete	+0·37
Posterior ethmoid foramen absent – foramen spinosum open	+0·32

The standard error of *r* is 0·10 in every case.

Table 4. *Measures of divergence between geographically separated populations*

Number of skulls classified		Nigeria (Ashanti)	Palestine (Lachish)	India (Punjab)	Burma	North America (British Columbia)	South America (Peru)
250	Egypt	0·026	0·045	−0·008	0·010	0·143	0·007
		0·009	**0·012**	—	**0·006**	**0·021**	**0·015**
56	Nigeria (Ashanti)	—	0·048	0·004	−0·009	0·178	0·074
		—	**0·015**	**0·004**	—	**0·030**	**0·019**
54	Palestine (Lachish)	—	—	0·027	0·040	0·202	0·167
		—	—	**0·012**	**0·014**	**0·032**	**0·029**
53	India (Punjab)	—	—	—	−0·014	0·101	0·045
		—	—	—	—	**0·023**	**0·015**
51	Burma	—	—	—	—	0·137	0.063
		—	—	—	—	**0·027**	**0·018**
50	North America	—	—	—	—	—	0·075
	(British Columbia)	—	—	—	—	—	**0·020**
53	South America (Peru)	—	—	—	—	—	—

(The figures in bold are estimates of the standard deviation.)

Palestinian sample has been included in Table 5 only because it is so small. The measure of divergence between the pooled males and females of all samples which had been reliably sexed was also calculated. This came out as 0·002 ± 0·004, i.e. there was no sex difference in variant incidence. The same position holds in the mouse, and greatly simplifies the analysis of data.

Table 5. *Measures of divergence between Egyptian (and neighbouring) populations of different antiquities*

Number of skulls classified	Approximate date	Predynastic	Early dynasties	12th–18th dynasties	26th–30th dynasties	Christian	Palestine	
							Lachish	Modern
28 Badarian	4100 B.C.	0·026	0·009	0·036	0·015	0·064	—	—
		0·015	**0·009**	**0·016**	**0·010**	**0·022**	—	—
36 Pre-dynastic	3500 B.C.	—	0·006	0·021	0·015	0·057	—	—
		—	**0·007**	**0·012**	**0·010**	**0·019**	—	—
29 Early dynasties	2800 B.C.	—	—	0·015	0·000	0·022	—	—
		—	—	—	0·002	0·013	—	—
55 12th–18th dynasties	1500 B.C.	—	—	—	0.012	0·007	0·062	—
		—	—	—	**0·008**	**0·006**	**0·018**	—
50 26th–30th dynasties	400 B.C.	—	—	—	—	0·006	—	—
		—	—	—	—	**0·006**	—	—
52 Christian	A.D. 200	—	—	—	—	—	—	0·071
		—	—	—	—	—	—	0·027
18 Palestine (Lachish)	700 B.C.	—	—	—	—	—	—	0·003
		—	—	—	—	—	—	**0·006**
54 Palestine (Modern)	—	—	—	—	—	—	—	—

(The figures in bold are estimates of the standard deviation.)

DISCUSSION

(1) *Anthropological*

The work described in this paper has obvious implications for anthropologists, particularly any who work with non-living populations which cannot be characterized serologically. However, it would be foolhardy to draw any major conclusions from the data in Table 4. The populations were classified to test the feasibility of a method, and were chosen for their availability rather than their anthropological significance. Nevertheless, a few comments are in order.

In general terms, the incidence of the characters that we have used are close to published values for similar populations (see Brothwell's 1963, 1965 reviews). For example, Berry (1967, following Brothwell, 1958) was able to include all the known frequencies of metopism, including the ones reported in this paper, on a map of the world, and to draw thereon approximate 0, 5 and 10 % isoincidence lines of the variant. This means that the scoring of variants by different workers appears to be comparable. However, we could not claim that uniformity in scoring some of the variants (for example, nos. 16, 27, 29) would be achieved by all people, although a single individual should be consistent in his own classification. The one major discrepancy between our results and published values concerns the incidence of palatine torus. We scored this character as present in only a single skull—a Burmese one. Stieda (cited by Le Double, 1906) reported palatine tori as occurring in 56 % of 229 Peruvian skulls, and 18·9 % of 227 Africans (of 'mixed races'). However, Russell (1900) classified the character as present in only 0·2 % of 436 Peruvian skulls (and in 19 % of Eskimos compared with Stieda's value of 60 %). It would seem that there are two distinct entities that can be scored as 'palatine torus'.

It is clear from Table 4 that the most distinct population is the North American one. This was composed of a group of Amerindians collected apparently somewhat haphazardly from the neighbourhood of Vancouver. The simplest assumption to make about them is that they were a local tribe, perhaps very limited in its distribution, and descended from only a few founders. The persistence of the characteristics of a small and perhaps atypical group of ancestors of a population is well-documented from gene frequency studies in different types of isolate (e.g. Critchley, 1934; Glass, 1954; Dean, 1963), and has been shown in the mouse studies of epigenetic variants (Berry, 1964). Other rather odd values in Table 4 are the greater likeness of the Egyptians to the Ashanti of Nigeria than to the inhabitants of Lachish in Palestine, and the lack of distinctiveness between West Africans and North Indians. For any critical anthropological arguments to be based on measures of divergence, it will be necessary for several neighbouring groups to be compared to determine the extent of regional variation, and to check the possibility of any one sample being derived from an atypical isolate.

The Egyptian data (Tables 2 and 5) are easier to interpret. First, there is an overall stability in the incidences of most variants, showing that the 'Egyptian stock' has persisted down the centuries, despite repeated incursions by other nations. It is, moreover, distinct from the two Palestinian populations, which again, are very similar to each other. Secondly, there is a general tendency for populations separated by a long span of time to be more morphologically dissimilar than those which are

close together in time. Thirdly, the biggest divergence between two adjacent (in time) populations occurred between the XII–XVIIIth and XXVI–XXXth dynasty samples (with the exception of the Badarian-Predynastic comparison)—a time when there was considerable trading and penetration of foreigners into Egypt. Lastly, the early Badarian population is somewhat peculiar in the results of its comparisons. Archaeologically, the position of the Badarian civilization is not certain (Arkell & Ucko, 1965), and it is hoped that work in progress on the skull variation of other early Egyptian populations may help to clear up some of the relationships between predynastic groups.

There is no doubt that epigenetic variant incidences have considerable advantages over morphological measurements for many anthropological purposes. In practical terms the lack of age, sex and inter-character correlations make the computation of multivariate statistics much simpler than is the case for metrical characters; scoring of variation is quick and easy; and there are grounds for believing that measures of divergence more accurately reflect genetical differences than statistics calculated from metrical data (Berry & Smith, 1968).

(2) *Anatomical*

On average every one of the skulls classified by us possessed three or four different variants. This variation must represent considerable genetical heterogeneity both within and between populations, although it is impossible to be specific about the extent and meaning of this heterogeneity. Nevertheless, it is important to recognize the prevalence of this genetically determined variation, because the variants we have been studying can be regarded as the pleiotropic manifestations of allelomorphs which also affect physiological competences (Grüneberg, 1955; Berry, 1965). In other words, the trivial morphological characters described in this paper may be markers reflecting the different disease and climatic tolerances of different peoples.

Furthermore, every epigenetic variant is an indicator of an embryological process, and the variants possessed by any one individual are a record of certain aspects of his development. We do not know at the moment what processes are primarily affected by the allelomorphs which influence the epigenetic variants, nor at what times during development these processes are acting. Nevertheless, epigenetic variation gives us an opportunity to study embryology without actually dealing with embryos, and to compare allometric patterns in different populations (cf. Trotter & Gleser, 1952, 1958). This could give us important information about human genetical architecture (King, 1959), and, perhaps more realistically, help in our understanding of the aetiology of congenital disease (Searle, 1958; Edwards, 1960).

SUMMARY

A considerable amount of normal discontinuous variation exists in the human skeleton. This variation is inherited, although it is actually determined by developmental (epigenetic) thresholds, rather than by straightforward gene action in the way that gene action is usually understood. This paper describes the incidence of thirty epigenetic variants in 585 crania from eight different localities, and points out some of the anthropological and anatomical implications of being able to genetically characterize populations in this way.

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REFERENCES

ARKELL, A. J. & UCKO, P. J. (1965). Review of predynastic development in the Nile valley. *Current Anthropology* **6**, 145–166.

ANDERSON, J. E. (1967). Skeletal "anomalies" as genetic indicators. *In* Brothwell, D. R. (*Ed.*). *The Skeletal Biology of Earlier Human Populations*. London: Pergamon. (In the Press).

BATRAWI, A. & MORANT, G. M. (1947). A study of a first dynasty series of Egyptian skulls from Sakkara and of an eleventh dynasty series from Thebes. *Biometrika* **34**, 18–27.

BERRY, R. J. (1963). Epigenetic polymorphism in wild populations of *Mus musculus*. *Genet. Res.* **4**, 193–220.

BERRY, R. J. (1964). The evolution of an island population of the house mouse. *Evolution* **18**, 468–483.

BERRY, R. J. (1965). Genetical change in an island mouse population. (Abstr.) *Ann. hum. Genet.* **29**, 110.

Berry, R. J. (1967). The biology of non-metrical variation in mice and men. *In* Brothwell, D. R. (*Ed.*). *The Skeletal Biology of Earlier Human Populations*. London: Pergamon. (In the Press).

BERRY, R. J. & SMITH, C. A. B. (1968). The genetical characterization of rat populations from skeletal data. (In manuscript.)

BROTHEWLL, D. R. (1958). The use of non-metrical characters of the skull in differentiating populations. *Dt. Ges. Anthrop.* **6**, 103–109.

BROTHWELL, D. R. (1963). *Digging up Bones. The Excavation, Treatment and Study of Human Skeletal Remains*, pp. 192. London: British Museum (Natural History).

BROTHWELL, D. R. (1965). Of mice and men. Epigenetic polymorphism in the skeleton. *In* Caso, A. *et al.* (*Eds.*). *Homenaje a Juan Comas en su 65 Aniversaria*, **2**, 9–21. Mexico.

CHAMBELLAN, M. (1883). *Étude Anatomique et Anthropologique sur les Os Wormiens*. Thesis, Paris. Cited by Dorsey, 1897.

CRITCHLEY, M. (1934). Huntington's Chorea and East Anglia. *J. S. Med.* **42**, 575–587.

DEAN, G. (1963). *The Porphyrias: a Story of Inheritance and Environment*, pp. 117. London: Pitman Medical.

DEOL, M. S., GRÜNEBERG, H., SEARLE, A. G. & TRUSLOVE, G. M. (1957). Genetical differentiation involving morphological characters in an inbred strain of mice. I. A British branch of the C 57 BL strain. *J. Morph.* **100**, 345–376.

DEOL, M. S. & TRUSLOVE, G. M. (1957). Genetical studies on the skeleton of the mouse. XX. Maternal physiology and variation in the skeleton of C 57 BL mice. *J. Genet.* **55**, 288–312.

DORSEY, G. A. (1897). Wormian bones in artificially deformed Kwakiutl crania. *Am. Anthrop.* **10**, 169–173.

EDWARDS, J. H. (1960). The simulation of Mendelism. *Acta genet. Statist. med.* **10**, 63–70.

FISHER, R. A. (1936). 'The coefficient of racial likeness' and the future of craniometry. *Jl R. anthrop. Inst.* **46**, 57–63.

GLASS, B. (1954). Genetic changes in human populations, especially those due to gene flow and genetic drift. *Adv. Genet.* **6**, 95–139.

GRAHNÈN, H. (1956). Hypodontia in the permanent dentition. A clinical and genetical investigation. *Odont. Revy.* **7**, suppl. 3.

GREWAL, M. S. (1962). The rate of genetic divergence in the C 57 BL strain of mice. *Genet. Res.* **3**, 226–237.

GRÜNEBERG, H. (1951). The genetics of a tooth defect in the mouse. *Proc. R. Soc.* B, **138**, 437–451.

GRÜNEBERG, H. (1952). Genetical studies on the skeleton of the mouse. IV. Quasi-continuous variations. *J. Genet.* **51**, 95–114.

GRÜNEBERG, H. (1955). Genetical studies on the skeleton of the mouse. XV. Relations between major and minor variants. *J. Genet.* **53**, 515–535.

GRÜNEBERG, H. (1963). *The Pathology of Development*. Chapters 12, 13. Oxford: Blackwell.

HESS, L. (1945). The metopic suture and the metopic syndrome. *Hum. Biol.* **17**, 107–136.

JOHNSON, C. C., GORLIN, R. J. & ANDERSON, V. E. (1965). Torus mandibularis: a genetic study. *Am. J. hum. Genet.* **17**, 433–442.

KING, J. C., (1959). Differences between populations in embryonic developmental rates. *Am. Nat.* **93**, 171–180.

LAUGHLIN, W. S. (1963). Eskimos and Aleuts: their origins and evolution. *Science*, **142**, 633–645.
LAUGHLIN, W. S. & JORGENSEN, J. B. (1956). Isolate variation in Greenlandic eskimo crania. *Acta genet. Statist. med.* 6, 3–12.
LE DOUBLE, A. F. (1903). *Variations des Os du Crane*, pp. 400. Paris: Vigot.
LE DOUBLE, A. F. (1906). *Variations des Os de la Face*, pp. 471. Paris: Vigot.
Le DOUBLE, A. F. (1912). *Variations de la Colonne Vertebrate de l'Homme*, pp. 543. Paris: Vigot.
MØLLER-CHRISTENSEN & SANDISON, A. T. (1963). Usura orbitae (cribra orbitalia) in the collection of crania in the Anatomy Department of the University of Glasgow. *Path. Microbiol.* **26**, 175–183.
MONTAGU, M. F. A. (1937). The medio-frontal suture and the problem of metopism in the primates. *Jl R. anthrop. Inst.* **67**, 157–201.
MORANT, G. M. (1925). A study of Egyptian craniology from prehistoric to Roman times. *Biometrika* **17**, 1–52.
RISDON, D. L. (1939). A study of the cranial and other human remains from Palestine excavated at Tell Duweir (Lachish) by the Wellcome-Marston archaeological research expedition. *Biometrika* **31**, 99–166.
ROCHE, A. F. (1964). Aural exotoses in Australian aboriginal skulls. *Ann. Otol. Rhinol. Lar.* **73**, 1–10.
RUSSELL, F. (1900). Studies in cranial variation. *Am. Nat.* **34**, 737–747.
SEARLE, A. G. (1954*a*). Genetical studies on the skeleton of the mouse, IX. Causes of skeletal variation within pure lines. *J. Genet.* **52**, 68–102.
SEARLE, A. G. (1954*b*). Genetical studies on the skeleton of the mouse. XI. The influence of diet on variation within pure lines. *J. Genet.* **52**, 413–424.
SEARLE, A. G. (1958). The incidence of anencephaly in a polytypic population. *Ann. hum. Genet.* **23**, 279–288.
SEARLE, A. G. (1964). Effects of low-level irradiation on fitness and skeletal variation in an inbred mouse strain. *Genetics*, **50**, 1159–1178.
SELBY, S., GARN, S. M. & KANAREFF, V. (1955). The incidence and familial nature of a bony bridge on the first cervical vertebra. *Am. J. phys. Anthrop.* (N.S.), **13**, 129–141.
SUZUKI, M. & SAKAI, T. (1960). A familial study of torus palatinus and torus mandibularis. *Am. J. phys. Anthrop.* (N.S.) **18**, 263–272.
TILDESLEY, M. L. (1920–21). A first study of the Burmese skull. *Biometrika* **13**, 176–262.
TORGENSEN, J. (1952). Genetic dynamics of human evolution. *Trans. 4th int. Congr. Anthrop. Ethnol.*, 98–102. Vienna.
TROTTER, M. & GLESER, G. C. (1952). Estimation of stature from long-bones of American Whites and Negroes. *Am. J. phys. Angtrop.* (N.S.), **10**, 463–514.
TROTTER, M., & GLESER, G. C. (1958). A re-evaluation of estimation of stature based on measurements taken during life and long-bones after death. *Am. J. phys. Anthrop.* (N.S.), **16**, 79–123.
TRUSLOVE, G. M., (1961). Genetical studies on the skeleton of the mouse. XXX. A search for correlations between some minor variants. *Genet. Res.* **2**, 431–438.
WOOD-JONES, F. (1930–31). The non-metrical morphological characters of the skull as criteria for racial diagnosis. I, II, III. *J. Anat.* **65**, 179–195; 368–378; 438–445.
WOOD-JONES, F. (1933–34). The non-metrical morphological characters of the skull as criteria for racial diagnosis. IV. *J. Anat.* **68**, 96–108.